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EFFECT OF COMPOUNDS WITH VARIOUS REDOX POTENTIALS ON THE PHOTOSYNTHESIS AND RESPIRATION OF ELODEA

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In prior work done at our laboratory the capacity of chlorophyll to be reversibly photoreduced by a number of compounds was shown [1, 2]. The possibility of the transfer of hydrogen (~~of~~ or an electron) by the active photoreduced form of chlorophyll to oxidized forms of prosthetic groups of ~~dehydrases~~ dehydrogenases (riboflavin and diphosphopyridine-nucleotide) ~~and~~ as well as to some dyestuffs was also demonstrated [3,4,5]. On the basis of these experiments the assumption was made that ~~dehydrases~~ dehydrogenases connect the photochemical stage with the dark stage of photosynthesis, taking up active hydrogen (or an electron) from the photoreduced form of chlorophyll and transferring it to the system of those enzymatic reactions of the dark stage ~~that~~ which lead to the binding and reduction of carbon dioxide [3]. ~~The~~ The dehydrogenase activity of chloroplasts was established in the work of N.M.Sisakyan et al [6].

In order to obtain data on the possible nature of intermediate systems which govern the transfer of hydrogen (or electrons) in the process of photosynthesis occuring in the living cells, we set up experiments in which the effect of various compounds on the photosynthesis and respiration of elodea was investigated.

1. The Compounds Investigated.

We investigated the effect of the following groups of compounds:

1. Dyestuffs active in relation to the ~~the~~ living plant, i. e. redox indicators which are reversibly reduced by the active hydrogen of metabolic products;

2. Antibiotics which in all probability selectively poison enzymatic systems;

3. Compounds that participate in biochemical redox processes, i. e. ascorbic acid, riboflavin, diphosphopyridine-nucleotide (DPN) as well as certain inorganic ions like NO_3', NO_2', and Fe^{+++}.

In the majority of cases, chemically pure, crystalline, reagent grade substances were used without supplementary purification. p-Quinone was resublimed before use. ~~Phenol-indophenol~~ [hydroxyphenyl-indophenol] was synthesized in the laboratory by the modified method of Heller [6]. DPN was isolated from baker's yeast according to a published method [8]. The DPN, as determined spectrophotometrically in our preparations (~~by the~~ from the value of the coefficient of extinction at 340 mμ) had a concentration of 15-16%. The solution of dehydroascorbic acid was obtained by oxidizing ascorbic acid with oxygen of the air over activated carbon /9/. The concentration of dehydroascorbic acid was determined ~~was determined~~ by titrating with dichlorophenol-indophenol ~~of the~~ the acid which had been reduced with H_2S (after H_2S had been removed by blowing nitrogen through the solution)

As far as antibiotics are concerned, a solution of Gramicidin S and crystalline penicillin and streptomycin were used.

2. Method of Measuring Photosynthesis and Respiration.

The oxygen metabolism of elodea in respiration was measured according to Warburg's manometric method with a carbonate-bicarbonate buffer. In this procedure the changes of gas pressure in the vessel are caused by oxygen metabolism only, because the partial pressure of CO_2 remains constant. The experiments were conducted at 25° in flat vessels ~~of~~ having a special shape and equipped with a side elbow and outlet (Fig 1). Illumination was carried out through an RO-2 ~~5-mm~~ red filter (5 mm) by means of a 150 wt lamp placed in a constant temperature bath at a distance of 6 cm from the vessels. Into ~~the~~ each vessel were placed a 1 g ~~bough~~ twig of elodea together with 10 ml of the carbonate-bicarbonate buffer having a p_H of 9.06 (8.5 ml of 0.1 M $NaHCO_3$ + 1.5 ml of 0.1 M Na_2CO_3). One ml of the compound to be investigated was introduced through the side outlet. Two parallel experiments were conducted. After thermostating in darkness for 12 min, the absorption of oxygen by respiration was measured. Then ~~Thereupon~~ the vessel was placed above the lamp and the gas metabolism due to photosynthesis measured for 12 min, whereupon the ~~compound~~ substance to be investigated was added ~~through~~ from the side ~~outlet~~ elbow and the gas metabolism measured for 30 min. Finally the vessels were again placed in darkness and the gas metabolism was measured in darkness in the presence of the substance being investigated.

In another series of experiments, the respiration and photosynthesis of elodea were measured after the plant had been previously treated with an aqueous solution of the substance under investigation. Five grams of elodea were kept for 30 min in 50 ml of a solution of a ~~the~~ dyestuff ~~solution~~ or some other compound ~~having~~ contained in a concentration of 10^{-3} or 10^{-4} M, in the solution. After the plant specimens ~~had been~~ treated in this manner had been rinsed with water once, manometric experiments were carried out immediately. Control experiments were performed without previous soaking. ~~The substances used in these experiments were selected~~ Experiments of this type can be carried out only with substances which do not absorb light in the range of wave lengths transmitted by light filter RO-2 (red threshhold 620 mμ), ~~in order~~ so that the screening influence of the filters on the absorption of light by chlorophyll is ~~be~~ eliminated.

The data listed in the tables were obtained in the following manner.

As can be seen from Fig 2, the process of oxygen resorption in respiration both before and after addition of the substances under investigation is rectilinear, while its velocity is expressed by the ~~an~~ tangent of the angle of inclination of the straight line to the axis of abscissae. Comparison of the tangents of angles of inclination of the straight lines of respiration permits to evaluate the effect of added substances on the rate of oxygen resorption in respiration. The initial rate of this process prior to photosynthesis, expressed by tg α (cf Fig 3), is assumed to be 100%. The change in this rate after photosynthesis, expressed in percent, will then be $\frac{tg\,\beta}{tg\,\alpha}$ 100.

The process of the evolution of oxygen in photosynthesis proceeding without any additions is also expressed by a straight line, the tangent of ~~f~~ whose angle of inclination to the axis of abscissae corresponds to the rate of the process. The observed evolution of oxygen under illumination corresponds ~~to-th~~ additively to the total gas metabolism of both photosynthesis and respiration; therefore the actual rate or velocity of oxygen evolution in photosynthesis will be expressed by the difference tg α' − tg α. In making these deduction~~s~~ we assumed that the respiration is the same in darkness and under illumination. After the substance under investigation ~~in-dyestuffs~~ has been added, the evolution of oxygen does not always proceed along a straight line. [in the case of dyestuffs] This apparently is due to the fact that the quantity of dyestuff which has diffused into the plant cells increases with time.

In cases where the course of photosynthesis is expressed by a straight line, the change of velocity under the influence of the added substance corresponds to

$$\frac{tg\,\beta' - \left(-\frac{tg\,\alpha + tg\,\beta}{2}\right)}{tg\,\beta - (-tg\,\alpha)} \cdot 100$$

where the mean value of ~~respiration~~ the gas metabolism of respiration before and after the addition is taken into consideration.

In cases where the process proceeds along a curved line, the rate of the process is assumed by definition to ~~assume~~ be equal to the slope at a point which corresponds to the 30 th minute on the curve of the gas metabolism of photosynthesis.

Fig 3 illustrates the method of calculation for neutral red with a concentration of 10^{-2}M in the side ~~outlet~~ elbow of the vessel. For the sake of clarity, the initial points of both processes involved were made to coincide ~~(in the origin~~ (for respiration processes, in origin O, and for photosynthesis processes, in origin O'). Tg α expresses the rate of the initial process of respiration; tg β, the rate of the final respiration; tg α', the rate of photosynthesis before addition of the substance; tg β', the rate of photosynthesis after addition of the substance. If the rate of the initial process of respiration is assumed to be 100%, the ~~final rate of respirat~~ final respiration will be 2.6/2.4 X 100=108%, i. e. the acceleration of the respiration process produced by the addition of neutral red lies within the limits of experimental error. The rate of photosynthesis before addition of the substance under investigation is composed ~~from~~ of the perceptible photosynthesis and the respiration, i. e. $tg\,\alpha' = (-tg\,\alpha) = 19.4 - (-2.4) = 21.8$. This value ~~In other words~~ is assumed to be 100%. The rate of photosynthesis after introduction of the substance represents the difference between measured photosynthesis and respiration, i. e. $tg\,\beta' - \left(\frac{tg\,\alpha + tg\,\beta}{2}\right) = 6.4 - (-2.5) = 8.9$

In other words, introduction of neutral red lowers photosynthesis to 41% of its original value.

The margin of error is estimated at ± 10%, in view of the fact that the experiments were carried out on plant material, the stability of which is influenced by many external causes.

III. Action of Dyestuffs and Quinone on the Photosynthesis and the Respiration of Elodea.

The following compounds, which cover ~~the range~~ redox potentials ranging in value from +0.3 to -0.3 v, were selected: quinone, phenol-indophenol, thionin, Nile blue, riboflavin, safranin T, neutral red. All these compounds, with the exception of quinones and safranine T, are dyestuffs which are active with respect to the living cell. As far as Nile blue is concerned, there is apparently a screening effect, but it is not quite clear whether the grains of chlorophyll are dyed by this substance. Phenol-indophenol is blue at $p_H = 9$ and red at $p_H = 6$; therefore only [preliminary] dyeing experiments were carried out with this substance.

The absorption spectra of the dyestuffs were measured in water at $p_H = 6$ and in the carbonate-bicarbonate buffer at $p_H = 9.08$ (Fig 4). In some special experiments the effect of the oxidized and the reduced form of pairs such as quinone-hydroquinone was investigated. The application of leuco-compounds of dyestuffs was impossible because of their rapid oxidation by oxygen of the air. Investigation of the action of hydroquinone by the method of pouring it in was ~~was~~ inconvenient, because this substance is rapidly oxidized at $p_H = 9$. Quinone is also oxidized under these conditions, so that in connection with the series of experiments where a solution of the substance under investigation is poured in, ~~a~~ control experiments without plant specimens were carried out. The control experiments with all compounds except those indicated [as easily oxidizable] above showed that only an insignificant consumption of oxygen took place.

After the experiments the dyed leaves were examined both under an ordinary and a fluorescence microscope (in the latter case, under excitation with mercury lines at 366 m μ). Notwithstanding the change in the color of some dyestuffs ~~on~~

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in a medium with $p_H = 9.08$, the color of the cells corresponded to p_H 6-7. A noticeable reduction of the red fluorescence of chloroplasts was observed only in the cases of quinone and thionine.

The experiments were carried out with 10^{-2} and 10^{-3} M concentrations of the dyestuffs in the side elbow space of the vessels, which corresponds to 10^{-3} and 10^{-4} M concentrations in the central space.

We made an attempt to estimate what quantity of dyestuff penetrates into the elodea cells. For this purpose 10^{-3} and 10^{-4} M solutions of the dyestuffs were prepared. Five grams of elodea were dipped into 50 ml of every dyestuff solution for 30 min. The coefficient of extinction of the dyestuff solution before and after the dyeing was measured and the amount of dyestuff adsorbed was calculated. The quantity of adsorbed dyestuff varied between $2 - 5 \times 10^{-6}$ mols/g of elodea with an initial concentration of 10^{-3} M and between $1 - 3 \times 10^{-8}$ mols/g of elodea with an initial concentration of 10^{-4} M.

Preliminary treatment of elodea with 10^{-3} M solutions of quinone or phenol-indophenol brings about a strong suppression of photosynthesis (to the level of 5-10% of that shown by the control), but has no effect on the respiration, just as in the experiments where the solutions are added by pouring in (Fig 5). At a 10^{-3}M concentration these compounds have practically no effect on either photosynthesis or respiration; there also was no apparent effect of hydroquinone on either process at the concentrations 10^{-3} and 10^{-4} M.

Preliminary treatment (dyeing) with solutions of dyestuffs stimulates respiration and suppresses photosynthesis in the following order: 1) neutral red; 2) safranine T; 3) Nile blue; 4) thionine. Neutral red has a weak effect on photosynthesis and respiration, while thionine strengthens respiration considerably and suppresses photosynthesis to a great extent.

IV. Action of Compounds Which Participate in Biochemical Redox Systems On the Photosynthesis and Respiration of Elodea.

The following compounds were investigated: ascorbic acid, dehydroascorbic acid, diphosphopyridine-nucleotide, and riboflavin. The effect of the ions NO_3', NO_2', and F^{+++} was also investigated (Fig 2).

Our experiments did not confirm the data of Bukatsch [10] in regard to the stimulating effect of ascorbic acid on photosynthesis; however, there was some stimulation of respiration by dehydroascorbic acid.

Introduction of DPN, riboflavin, or NO_3' did not exert a significant effect on either photosynthesis or respiration. Sodium nitrite lowers photosynthesis per appreciably and is presumably reduced at the expense of the photoreaction. The possible error in the data listed in Table 2 amounts to ± 10%.

V. Action of Antibiotics On the Photosynthesis and Respiration of Elodea.

In the search for selective inhibitors of photosynthesis and respiration, we also investigated the action of antibiotics. In the experiments in question, 5 g of elodea were soaked for 1 h in 25 ml of an aqueous solution of the antibiotic. Then the photosynthesis and respiration were determined by the manometric method described above. The concentration of penicillin and gramicidin S was 10^{-2}M, while that of streptomycin was 5×10^{-3}M. Penicillin and streptomycin have only a weak effect on the photosynthesis and respiration of elodea. Gramicidin S has no effect on respiration, but suppresses photosynthesis considerably (by 80%). It is possible that this effect is connected with the property of gramicidin to suppress dehydrogenases which has been shown in Popova's work [12]

Conclusions.

On the basis of the data obtained, the following conclusions can be made:

1. Suppression of photosynthesis by the dyestuffs investigated may be correlated with the values of their redox potential (E_o): the higher suppression effect is higher when E_o is more positive.

2. The action of a dyestuff on respiration is usually opposed to its action on photosynthesis; compounds having more highly positive values of E_o stimulate respiration.

Increase of the respiration of plant tissues under the action of some dyestuffs has been known for a long time: V.I.Palladin et al [13] originally established the strengthening of the respiration of plant tissues which had been dyed with methylene blue. In this process the reversibly reacting dyestuff functions as an an intermediate catalytic system which serves as an acceptor for the hydrogen (or electrons) of metabolites, and is then oxidized by the oxygen of the air.

The suppressing action on photosynthesis of the compounds investigated has the same explanation: hydrogen (or an electron) is taken up from photochemically formed active reduced substances, which have a much more negative potential than respiration metabolites, and then these substances are oxidised through the action of oxygen under intermediate formation of peroxides. Oxidases participate in this process. These reactions of the "capture" of hydrogen mobilized in the photochemical stage may be represented by the following scheme, from which the stage of semiquinone formation has been omitted:

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$$DH_2 + K \rightarrow D + KH_2$$
$$KH_2 + O_2 \rightarrow K + H_2O_2$$
$$H_2O_2 \rightarrow H_2O + 1/2\ O_2$$

where $D \rightleftharpoons DH_2$ is a dehydrogenase system or some other system which originally takes up the hydrogen of the reduced form of chlorophyll, and $K \rightleftharpoons KH_2$ is the reversible system dyestuff - leucocompound.

However, the usefulness of this scheme for explaining the observed suppressing action of quinone or phenol-indophenol on photosynthesis is doubtful. The reduced forms of these compounds are oxidized ~~reduced~~ with difficulty by the oxygen of the air in a neutral medium; this explains the application of quinones for measuring the photochemical activity of isolated chloroplasts. In this reaction there is reduction of quinone and evolution of molecular oxygen, which is practically not used at all for the oxidation of the reduced form of quinone or phenol-indophenol. Suppression of photosynthesis by these compounds may be ascribed either to the reaction of the appearing reduced forms with active peroxides that form in the course of photosynthesis, or else to the formation ~~of~~ from quinone in an aqueous medium of compounds which poison photosynthesis. The latter possibility has been mentioned in the literature [14].

The possibility of the interaction of the dyestuff with the photochemically formed compound DH_2 is determined by the values of their redox potentials. The value of the redox potential may be changed by adsorption of the dyestuff on cellular structures; here we operate only with E_o values corresponding to $p_H = 7$.

The E_o value of a dyestuff at which there is no longer any suppressing effect on photosynthesis will indicate the approximate E_o value of active reduced compounds which are formed in photosynthesis. The effect on photosynthesis of neutral red with an E_o of -0.32 v is already very small, which indicates that the E_o of DH_2 is in all probability higher than -0.32 v.

3. The absence of either a suppressing or stimulating effect on ~~the part~~ photosynthesis due to the presence of ~~by~~ oxidized forms of substances which participate in biochemical processes (dehydro-ascorbic acid, riboflavin, DPN) may be explained by the fact that the reduced modifications of these ~~compounds~~ substances participate ~~participate~~ in the biochemical reactions of photosynthesis upon formation. Other explanations are also possible, however. For instance, one may assume that the system of biochemical reactions which effects hydrogen transfer in the living cell is completely balanced, so that introduction of an excess of the compound in question does not bring about any observable effect.

4. The suppressing effect ~~of~~ exerted by gramicidin on photosynthesis, while other antibiotics are ineffective, may be regarded as an argument in favor of the

assumption that hydrogenases participate in photosynthesis.

5. In one of our former papers /5/ we showed that the photoreduced form of chlorophyll (in an isolated system) reacts in darkness with all investigated oxidising agents up to a value of E_0 = -0.32 v. This indicates that the reduction potential of the operating photosynthesis system and of the reduced form of chlorophyll ~~are~~ lie near to each other in value, which speaks in favor of the assumption that there is reversible photoreduction of chlorophyll in photosynthesis.

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Table 1. Effect of Dyestuffs, Quinone, and Hydroquinone on the Respiration and Photosynthesis of Elodea.

Name of substance	Maximum of absorption in the visible range ± 5 mμ		Redox potential in volts	Effect of substance in % at the concentration of			
				10^{-3}M		10^{-4}M	
	at p_H=6	at p_H= 9.08	E at p_H=[illegible]	respiration	photosynthesis	respiration	photosynthesis
Quinone	425	425	+0.29	105	4	98	90
Hydroquinone **	-	-	-	130	101	119	93
Thionine	600	600	+0.062	160	14	186	13
Nile blue	640	595*	-0.12	118	53	116	53
Safranine T	520	520	-0.29	92	15	91	51
Neutral red	525	455*	-0.33	105	41	106	100

* Precipitates from alkaline solution on standing.

** Data for hydroquinone were obtained by the method of preliminary treatment with solution.

Table 2. Action of Compounds and Ions Which Participate in Biochemical Redox Systems On the Photosynthesis and Respiration of Elodea.

Compound- Substance	Effect in % respiration	Effect in % photosynthesis	Concentration of the substance in M	Method of treatment
Ascorbic acid	105	95	10^{-3}	Preliminary treatment of elodea with solutions of the acids.
Dehydroascorbic acid	150	102	10^{-3}	
Riboflavin *	109	106	2×10^{-4}	Pouring in of solutions of the concentration indicated at the 12 th minute of photosynthesis.
DPN	110	103	10^{-2}	
$NaNO_3$	85	90	10^{-2}	
$NaNO_2$	10[illegible]	57	10^{-2}	
$Fe_2(SO_4)_3$	12	5[illegible]	(saturated)	

* The limiting concentration of riboflavin, which corresponds to its solubility in water, amounts to 2×10^{-4} M. The solubility of riboflavin is increased by the presence of nicotinic acid amide [11]. However, an experiment carried out with a 5% solution of nicotinic acid amide showed that this compound has a suppressing effect on photosynthesis.

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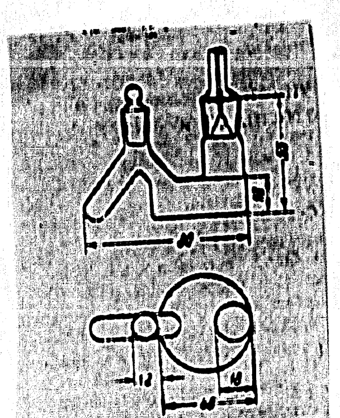

Рис. 1. Вид манометрического сосуда с плоским дном и боковым отводом

Fig. 1. Appearance of the Manometric Vessel With a Flat Bottom and Side Elbow With Outlet.

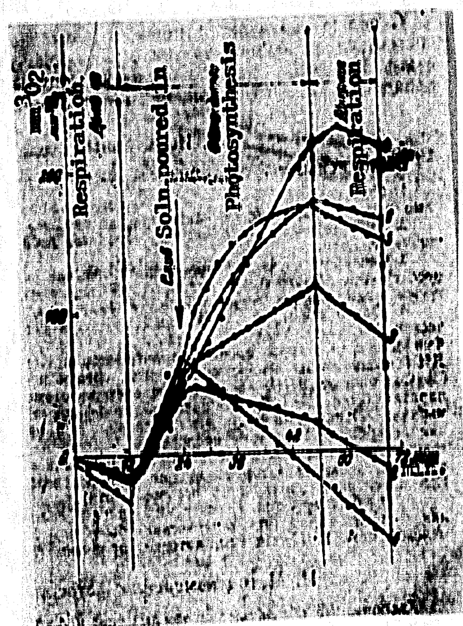

Fig. 2. Curves of Photosynthesis and Respiration of Elodea. Solutions of Dyestuffs Are Added From the Side Elbow of the Vessel at the 12 th Minute of Photosynthesis.

1 - quinone; 2 - thionine; 3 - Nile blue; 4 - ribiflavin; 5 - safranine T; 6 - neutral red. Concentration in the side elbow of the vessel is 10^{-2}M.

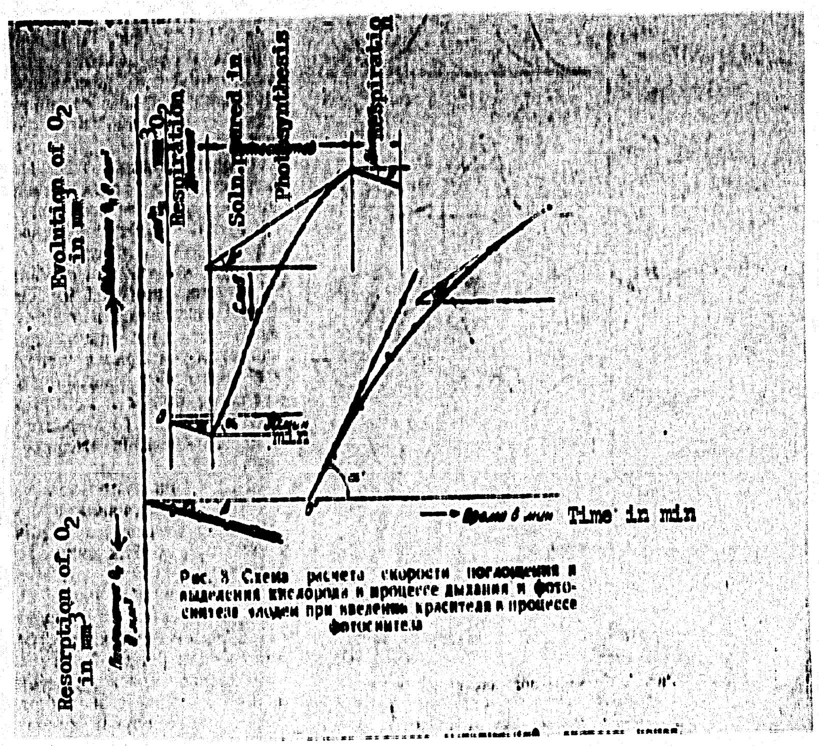

Рис. 3 Схема расчета скорости поглощения и выделения кислорода в процессе дыхания и фотосинтеза элодеи при введении красителя в процессе фотосинтеза

Fig 3. Scheme For Calculating the Rates of Resorption and Evolution of Oxygen in Respiration and Photosynthesis of Elodea Upon Introduction of the Dyestuff During the Process of Photosynthesis.

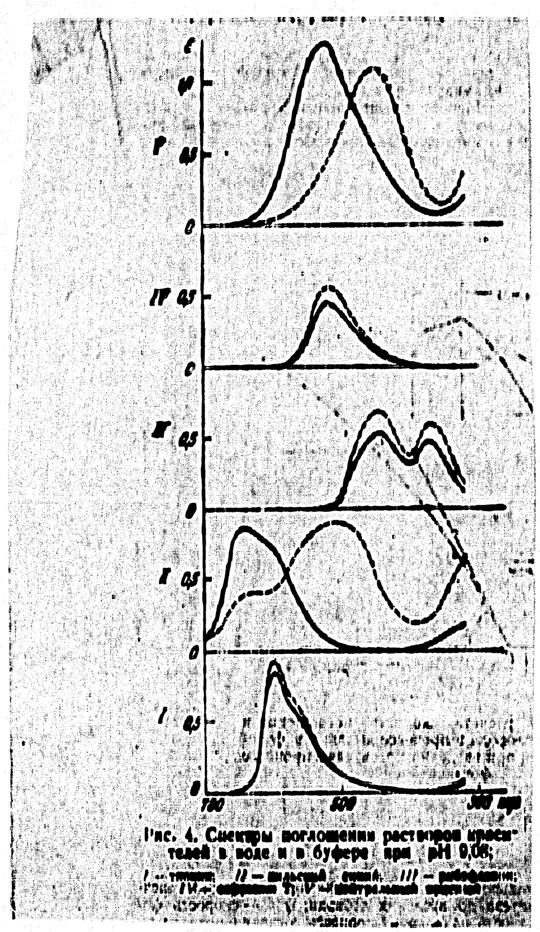

Fig. 4. Absorption Spectra of Dyestuffs in Water and in a Buffer Solution With p_H = 9.08.

I - thionone; II - Nile blue; III - ribovlavin; IV - safranine T; V - neutral red.

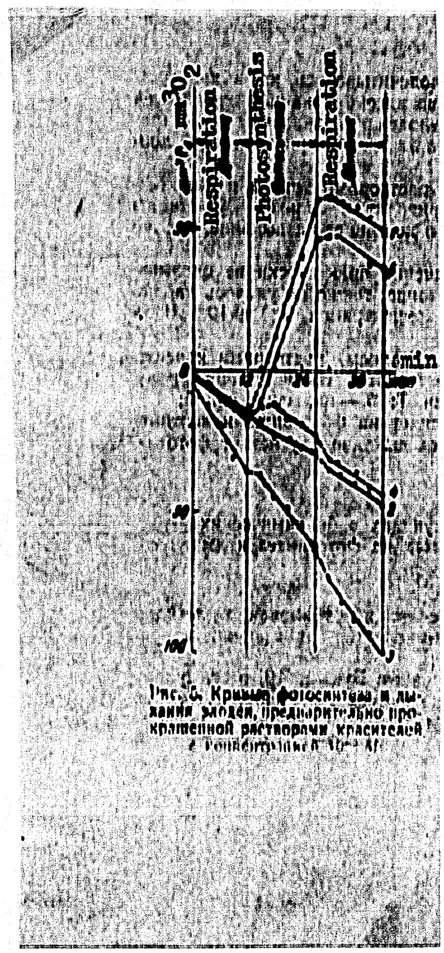

Fig 5. Curves of Photosynthesis and Respiration of Elodea Which Had Been Dyed With 10^{-3} Dyestuff Solutions Prior To the Experiments.

1 - control experiment carried out without preliminary treatment; 2 - quinine; 3 - thionine; 4 - phenol-indophenol; 5 - neutral red.

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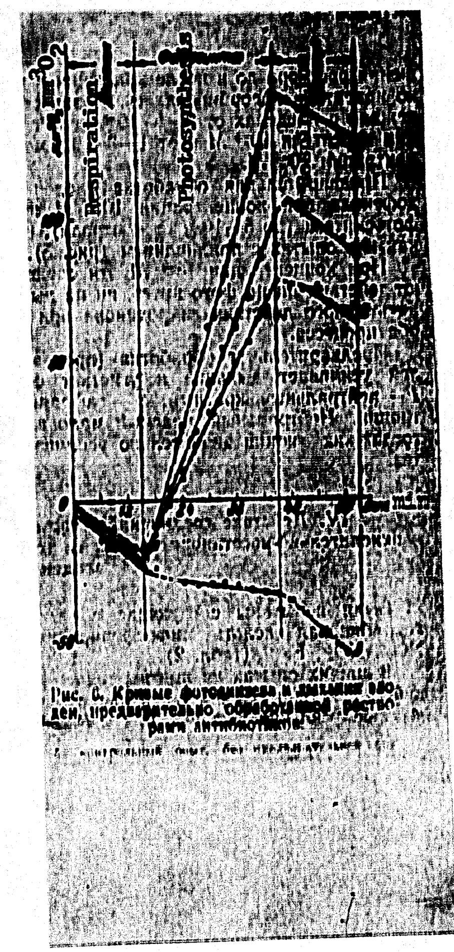

Fig 6. Curves of Photosynthesis and Respiration of Elodea Which Had Been Treated With Solutions of Antibiotics Prior to the Experiments.

1 = control experiment carried out without preliminary treatment; 2 = 10^{-2} M solution of penicillin; 3 = 0.7% (~10^{-2} M) solution of gramicidin; 4 = 5×10^{-3} M solution of streptomycin.

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